Growth of long-finned squid, *Loligo pealei*, in the northwest Atlantic

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Abstract.—The application of statolith ageing techniques to long-finned squid, *Loligo pealei*, suggests that this species has a life span of less than one year and grows more rapidly than previously thought. In this study we provide direct estimates of growth for long-finned squid in the northwest Atlantic based on a data set of 353 animals aged by counting putative daily statolith increments. We examine empirical patterns in length and weight at age and estimate parameters of a general growth model. The results indicate that growth rate increases rapidly as squid age and that growth in length and weight is exponential. Although there is substantial heterogeneity in *L. pealei* size at age, sexual dimorphism is evident: males grow more rapidly than do females and achieve larger sizes. Back-calculated hatching dates show that *L. pealei* spawning is not restricted to spring through late-autumn, as previously supposed, but occurs during winter months as well. Differences between growth rates of squid hatched during June–October and November–May are suggested and lend support to the hypothesis that growth can be influenced by seasonal environmental conditions. We discuss the practical implications of our findings for the assessment and management of the long-finned squid stock in the northwest Atlantic.

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The long-finned squid, *Loligo pealei* (also known as the longfin inshore squid (FAO, 1984), is a pelagic schooling loliginid distributed in continental shelf and slope waters from Newfoundland, Canada (Dawe et al., 1990), to the Gulf of Venezuela (Summers, 1983). A substantial commercial fishery exists in the northwest Atlantic where annual landings averaged 17,300 metric tons (t) during 1963–92, and totalled 22,300 t in 1993 for an ex-vessel value of approximately $30 million (NEFSC, 1995). Recent advances in the use of statolith increments to age squid directly and recent increases in fishing effort in the northwest Atlantic have led to a renewed interest in the life history of this species, and, in particular, its growth rate.

Several estimates of the growth rate of *L. pealei* have been made by comparing modes of length-frequency distributions (Verrill, 1881; Summers, 1968, 1971; Cohen, 1976; Mesnil, 1977; Whitaker, 1978; Lange, 1980; Lange and Sissenwine, 1980; Macy, 1980; Hixon et al., 1981). These studies generally have suggested that growth rate, measured by change in dorsal mantle length (ML), ranged from 10 to 24 mm per month, and that growth rate was dependent upon sex, hatching date, and season (Hixon et al., 1981). Sexual dimorphism was evident; males attained larger sizes than did females (Summers, 1971). Seasonal effects on growth were also suggested; higher growth rates occurred during summer months and lower rates during winter months (Mesnil, 1977). Latitudinal differences in age structure and mean size of *L. pealei* have also been proposed (Summers, 1971), namely that mean size has been suggested to be greater at higher latitudes. These studies, combined with the observed maximum size of approximately 46.5 cm mantle length (Summers, 1968), were consistent with a maximum life span of roughly three years in the northwest Atlantic, a value that was assumed for stock assessment (NEFSC, 1988).

The inferred growth rates of *L. pealei*, based on length-frequency analyses, should be viewed cautiously because they have not been supported by direct ageing data (Caddy, 1991). In general, growth rates of squid might be expected to vary with prey availability (O'Dor et al., 1980), temperature (Forsythe, 1993), and population density

(Dawe, 1988). Squid populations with protracted spawning seasons, such as that of *L. pealei* (Summers, 1971; Macy, 1980), can be composed of numerous broods or microcohorts that may experience different growth and survival rates (Caddy, 1991). As a result, length-frequency samples may consist of several microcohorts with differing growth rates. Migration of microcohorts with differing hatching dates and growth rates to and from an area (e.g. *Illex illecebrosus*, Dawe and Beck[1]; *Illex argentinus*, Arkhipkin, 1993a) may also substantially influence the size composition of a local population, and may bias growth estimates based on length-frequency data (Hatfield and Rodhouse, 1994). Further, postspawning mortality of squid may also influence local size composition if the sampled area is a spawning ground. For these reasons, analysis of length-frequency data may be inadequate in representing the potentially complicated pattern of individual growth within a squid population. Therefore, it is highly desirable to have a method to age individual squid directly.

Statolith ageing techniques (Jereb et al., 1991) have recently provided useful information on the age, growth, and population structure of several squid species (Rodhouse and Hatfield, 1990a; Jackson and Choat, 1992; Arkhipkin, 1993, a and b; Arkhipkin and Nekludova, 1993; Hatfield and Rodhouse, 1994). Ageing of squid, based on counts of fine increments presumed to have daily periodicity, was first developed for *Illex illecebrosus* (Lipinski, 1978) and *Loligo opalescens* (Spratt, 1979) in the late 1970's. Subsequently, studies of several species have indicated that increments within statolith microstructure are formed daily (Dawe et el., 1985; Hurley et al., 1985; Lipinski, 1986; Jackson, 1990, a and b; Jackson et al., 1993), although the mechanisms that regulate increment formation have not yet been determined (Jackson, 1994a).

The application of statolith ageing techniques to *L. pealei* suggests that this species has a life span of less than one year and grows more rapidly than previously thought (Macy, 1995; Macy[2]). In this study we provide estimates of growth rate for *L. pealei* in the northwest Atlantic based on a data set of 353 animals aged by counting putative daily increments on statoliths. We examine empirical patterns in length and weight at age and estimate parameters of a general growth model proposed by Schnute (1981) by squid sex and season of hatching. We discuss some practical implications of our findings for the assessment and management of the stock in the northwest Atlantic.

Materials and methods

Sampling

Data used in this growth study consisted of 353 squid collected during 1991–93. Squid samples were obtained from catches of a commercial fishing vessel[3] and from inshore research surveys in the northwest Atlantic (Table 1; Fig. 1). Samples were flash frozen and stored for subsequent analysis. Basic measurements of mantle length (ML) (to the nearest mm), wet weight (g), and morphometric characters needed to assess maturity stage according to the scheme of Macy (1982a) were taken. Statoliths were dissected from all animals and stored dry in plastic 96-well immunoassay microplates. Statoliths were randomly selected from representative size categories of squid on the basis of observed length-frequency distributions for male, female, and squid of indeterminate sex.

Statolith preparation

Statoliths were prepared by mounting them in a thermoplastic medium (Crystal Bond, Aremco Products; cf. Secor et al., 1991) and by grinding both anterior and posterior surfaces in a manner similar to that described by Jackson (1990a). Several steps were required to prepare a statolith for ageing (Fig. 2). First, a small piece of mounting medium was placed on a petrographic slide (26 × 46 mm) and melted with a hot-air gun. The statolith was then placed in the fluid medium with its concave anterior side down and allowed to cool (Fig. 2B). Material was ground from the exposed convex posterior surface (Fig. 2C) with a graded sequence (12 μm to 3 μm) of water-lubricated abrasive films (Imperial Brand lapping film, 3M Co.) to reveal the nucleus. Progress was monitored throughout the grinding procedure with a stereoscopic dissecting microscope. When the nucleus was clearly revealed, the exposed surface was polished with 0.3-μm aluminum oxide polish (Buehler micropolish) in water on a felt lapidary pad, rinsed with deionized water, and cleaned ultrasonically. After the posterior face was ground, the mounted

[1] Dawe, E. G., and P. C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. ICES Council Meeting, Shellfish Committee/K, 33 p.

[2] Macy, W. K., III. 1992. Preliminary age determination of the squid, *Loligo pealei*, using digital imaging. ICES, Shellfish Committee Council Meeting (mimeo), 9 p.

[3] FV *Huntress*, Deep Sea Fish Co., Point Judith, RI.

Table 1

Sample sizes of indeterminate-sex, female, and male long-finned squid, *Loligo pealei*, by collection date, location, source, and sampling gear. In the location field the map code refers to Figure 1. D.E.M. = Department of Environmental Management.

Collection dates	Location (map code)	Source	Sampling gear	Number of squid			
				Indeterminate-sex	Female	Male	Total
1991							
10 Apr	Block Island Sound (1)	Pt. Judith Fishermen's Coop.	Otter trawl[1]	—	7	7	14
10 May	Vineyard Sound (2)	Marine Biological Lab.	Otter trawl[2]	—	2	2	4
13–15 May	Block Island Sound (1)	Rhode Island D.E.M.	Otter trawl[3]	—	1	6	7
16–18 May	Narragansett Bay (1)	W.K. Macy	Dip net[4]	—	1	3	4
22 May	Block Island Sound (1)	Rhode Island D.E.M.	Otter trawl[3]	12	20	12	44
17–18 Jul	Narragansett Bay (1)	Rhode Island D.E.M.	Otter trawl[3]	31	8	6	45
31 Jul	Narragansett Bay (1)	W.K. Macy	Dip net[4]	—	1	2	3
15 Oct	Block Island Sound (1)	Rhode Island D.E.M.	Otter trawl[3]	28	25	27	80
1992							
1 Jan	Hudson Canyon (3)	F/V *Huntress*	Otter trawl[1]	—	—	1	1
9 Jan	Block Canyon (4)	F/V *Huntress*	Otter trawl[1]	—	—	5	5
31 Jan–2 Feb	Block Canyon (4)	F/V *Huntress*	Otter trawl[1]	—	—	2	2
17 Feb	Block Canyon (4)	F/V *Huntress*	Otter trawl[1]	—	—	1	1
11 Mar	Wilmington Canyon (5)	F/V *Huntress*	Otter trawl[1]	—	—	5	5
6–14 May	Narragansett Bay (1)	Univ. Rhode Island	Otter trawl[5]	—	27	23	50
7 Oct	Narragansett Bay (1)	Rhode Island D.E.M.	Otter trawl[3]	4	22	14	40
1993							
7 Feb	Hudson Canyon (3)	F/V *Huntress*	Otter trawl[1]	—	2	4	6
25 Feb–8 Mar	Hudson Canyon (3), Baltimore Canyon (6), and Lydonia Canyon (7)	F/V *Huntress*	Otter trawl[1]	1	22	19	40

[1] Mesh size not reported.
[2] 32-mm mesh.
[3] 6-mm mesh.
[4] Hand-held dip net with SCUBA gear.
[5] 19-mm mesh. Graduate School of Oceanography, Univ. Rhode Island, trawl survey described in Jeffries and Johnson (1974).

statolith was reheated to soften the medium and turned over with a pair of probes constructed of insect pins so that the anterior face could be ground (Fig. 2, C (2) and D). The statolith was oriented with the dorsal dome elevated and the anterior face was carefully ground. When the nucleus was clearly revealed, the anterior face was polished and cleaned.

Because the statolith of *L. pealei* grows outward from the oval-shaped nucleus in a curved manner (Fig. 2, A and B), a second grinding and polishing of the posterior surface (Fig. 2E) was generally needed to reveal the entire sequence of growth increments from the nucleus to the lateral dome (LD) margin. Because of this curvature, no single sectioning plane could have exposed all layers equally well. As a result, the use of the typical two-sided grinding method (Jackson, 1990a; Jereb et al., 1991) would have produced increments that were difficult to resolve. To circumvent this difficulty, the posterior surface was ground a second time (Fig. 2E) at a slightly different angle to approximate the curved statolith growth plane. For squid smaller than 2 cm ML, however, a single grinding of each surface was usually sufficient to reveal the statolith microstructure. After the second posterior grinding, the mounted statolith was reheated, and a thin film of fluid medium was smeared over the uppermost ground surface to improve transparency. As the medium cooled, the LD margin was elevated so that the last-ground plane was approximately parallel to the surface of the slide (Fig. 2F); this was done to improve the clarity of statolith microstructure under a 40× objective lens.

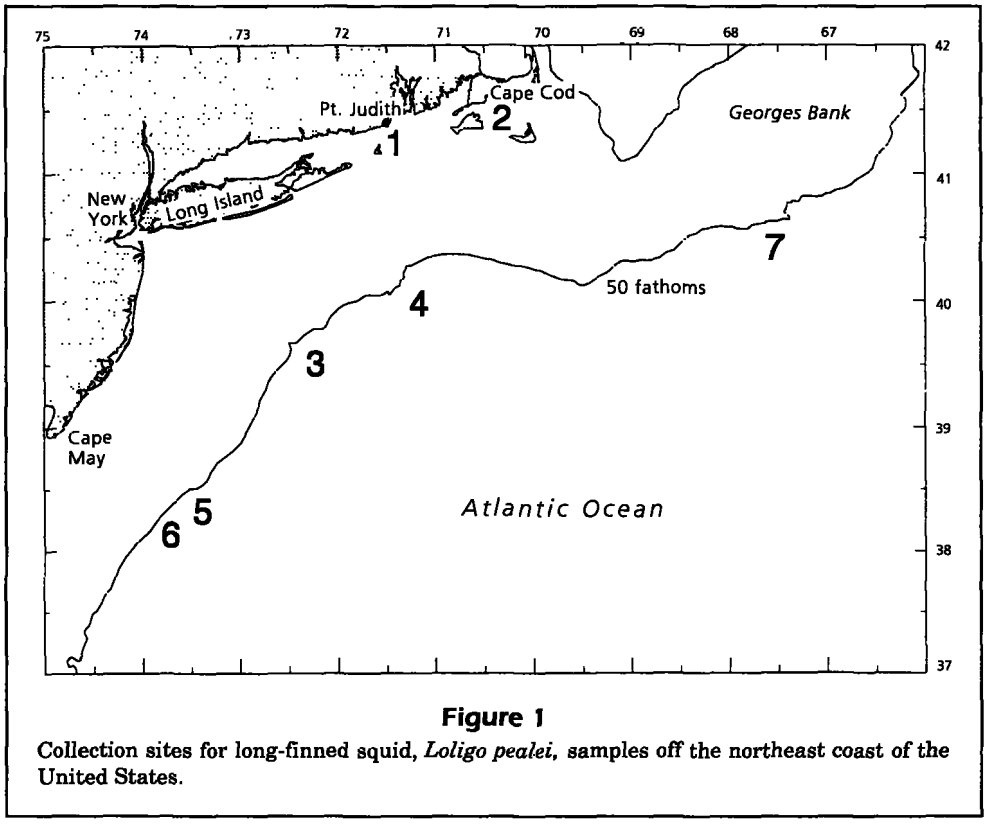

Figure 1

Collection sites for long-finned squid, *Loligo pealei*, samples off the northeast coast of the United States.

Statolith ageing

A video image processing system with high-resolution monochrome video camera (MTI-Dage 65, Newvicon) mounted on a compound microscope (Zeiss Universal) was used to count increments (Macy, 1995). Because of the low contrast seen in *L. pealei* statolith microstructure, image enhancement was employed to identify growth marks. Statolith increments were counted by using transmitted light with the microscope stage condenser (brightfield) set to the smallest aperture to obtain maximum depth of field. A rotatable polarizing filter was also placed above the field condenser to improve contrast between increments. Within a prepared *L. pealei* statolith, a series of paired bands that alternate from light to dark is observable in the LD, beginning at the nucleus and continuing to the LD margin. Two fractures that radiate outward from the nucleus are also apparent. These fractures are not the result of statolith preparation because they are also found in unprepared statoliths. In this study, the successive circumferential light bands in the statolith (appearing black in enhanced images) were counted and will be referred to hereafter as "growth increments."

Counting began with the first check or natal ring (Lipinski, 1986; Natsukari et al., 1988, Saleh-Eddine, 1991), which is a distinct oblong-shaped mark roughly the same size (100–120 μm) as the major axis length of a statolith from a *L. pealei* embryo. Although prehatching increments can sometimes be observed (Saleh-Eddine, 1991; Macy, 1995), their periodicity, if any, is unknown. Typically, counting proceeded along a series of transects extending outward from the first check across the LD to the edge. Up to six fields of view were used to enumerate the increments.

The consistency of increment counts between the reader of this study and another experienced reader was evaluated post hoc by using a sample of 76 *L. pealei* collected during 1994. Three statistical tests were applied to determine the consistency between age readings (cf. Campana et al., 1995): a linear regression analysis of paired counts; a paired *t*-test; and a paired Wilcoxon rank test. Results of the linear regression of one reader's counts on the other's indicated that the regression slope was not significantly different from 1 (b=1.046, σ_b=0.033, P=0.17) and that the regression intercept was not significantly different from 0(a=1.655, σ_a=4.697, P=0.73). This suggested that the readers' age determinations were consistent. Results of the paired *t*-test, however, indicated a significant mean paired difference of 7.6 days (σ=2.1, P<0.001). Similarly, results of the Wilcoxon signed rank test indicated a significant median paired difference (P<0.001) existed between

readers. The results of the statistical tests were equivocal but suggested that there was a potential bias between the readers' counts. However, the apparent bias was relatively small and did not suggest that there were substantial differences between the readers' recognition of increments.

An examination of *L. pealei* marked with oxytetracycline supported the hypothesis that statolith increments are formed daily (Macy, 1995). In particular, one marked squid that did grow appreciably during a 21-d period was found to have a total of 21 statolith increments (Macy, 1995). To date, the daily increment hypothesis has been verified by statolith marking for several squid species, including *Illex illecebrosus* (Dawe et al., 1985), *Alloteuthis subulata* (Lipinski, 1986), *Loligo opalescens* (Jackson, 1994b), *Sepioteuthis lessoniana* (Jackson, 1990a; Jackson et al., 1993), *Loliolus noctiluca* and *Loligo chinensis* (Jackson, 1990b), *Todarodes pacificus* (Nakamura and Sakurai, 1991), *Abralia trigonura* (Bigelow, 1992), *Ommastrephes bartramii* (Bigelow and Landgraf, 1993), *Onychoteuthis borealjaponica* (Bigelow, 1994), and validation is in progress for *Loligo plei*.[4] The daily increment hypothesis has also been verified by using laboratory-reared squid of known age for *Loligo opalescens* (Jackson, 1994b) and for *Sepioteuthis lessoniana* (Jackson et al., 1993), both loliginids, and is considered to be the best working hypothesis for statolith increment formation in *L. pealei* on the basis of limited marking data and by analogy with other loliginid species.

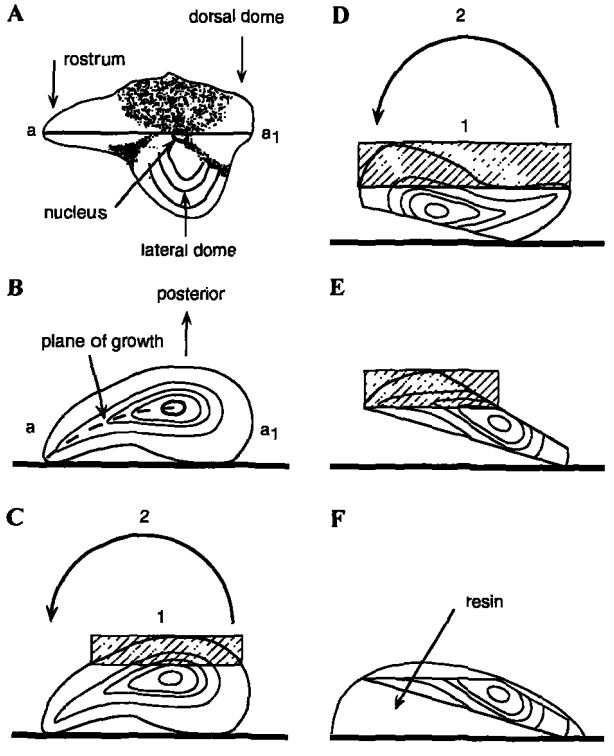

Figure 2

(**A**) Schematic view of posterior face of *Loligo pealei* statolith with a ventro–dorsal cross section indicated from points a to a_1. (**B**) Cross section [a, a_1] from (A) showing the curved plane where growth increments are counted. (**C**) After initial grinding removes the cross-hatched area to reveal the nucleus (1), the statolith is turned over (2). (**D**) After the anterior side of the statolith is oriented with the dorsal dome elevated and the cross-hatched material removed (1), the statolith is turned over again to show the posterior face (2). (**E**) The lateral dome is elevated while the resin cools and the cross-hatched material is removed. (**F**) The polished statolith is covered with molten resin and allowed to cool with the lateral dome elevated.

Month of hatching was backcalculated for all samples by subtracting the estimated age, based on statolith analysis, from the date of sample collection. Samples were categorized by sex (indeterminate, female, and male) and maturity stage (immature, maturing, and mature) to examine whether size at age was related to maturity stage. Samples were also categorized by month and year of hatching to examine monthly and seasonal patterns in size at age. Average monthly growth rates of individual squid were computed to examine individual variation in growth, where the growth rate in length was ML (mm) divided by age (months), and the growth rate in weight was total wet weight (g) divided by age. Summary statistics of the average monthly growth rate of individuals in ML and in weight were computed for squid categorized by sex, maturity stage, hatch month, and hatch year. Variances of growth rate in length and weight were log-transformed and tested for homogeneity by sex, maturity, hatch month, and hatch year by using Bartlett's test for homogeneity of variances (Sokal and Rohlf, 1981). Unplanned multiple comparison tests appropriate for equal variances and unequal samples sizes (Sokal and Rohlf, 1981) and for unequal variances and sample sizes (Games and Howell, 1976; Day and Quinn, 1989) were applied to test whether growth rate in length and weight differed by sex, maturity stage, hatch month, and hatch year.

Growth model

We applied the general growth model of Schnute (1981) to quantify the relationship between length

[4] Jackson, G. 1994. Department of Marine Biology, James Cook Univ., Townsville, Queensland 4811, Australia. Personal commun.

and weight at age for *L. pealei*. This flexible model includes asymptotic, linear, exponential, and other growth curves as particular cases. The complete set of size-at-age data consisted of the 353 squid that were aged. Size data for the i^{th} individual were denoted as (t_i, y_i), where t_i was observed age in months, and y_i is either observed length in centimeters or weight in grams. Additionally, t_{max} and t_{min} denoted the maximum and minimum observed age in months for any subset of the size-at-age data. In the most general case, the Schnute model has four parameters: α, β, y_{min}, and y_{max}. The parameters α and β determine the shape of the growth curve, whereas the parameters y_{min} and y_{max} are the predicted sizes of the youngest and oldest individuals in the subset of weight-at-age data. That is, $y_{min} = Y(t_{min})$ and $y_{max} = Y(t_{max})$, where Y is the growth model.

There are four general forms for the Schnute growth model. The most general form (case I) gives size (Y) at age (t) as

$$Y(t) = \left\{ (y_{\min})^{\beta} + \left((y_{max})^{\beta} - (y_{min})^{\beta}\right) \frac{1-\exp[-\alpha(t-t_{min})]}{1-\exp[-\alpha(t_{max}-t_{min})]} \right\}^{\frac{1}{\beta}}. \quad (1)$$

In Equation 1, it is assumed that $\alpha \neq 0$ and $\beta \neq 0$ and that $y_{min} > 0$ and $y_{max} > 0$. A second form (case II) sets the β parameter to be 0 in the differential equation defining $Y(t)$. The resulting 3-parameter model is

$$Y(t) = y_{min} \exp\left[\ln\left(\frac{y_{max}}{y_{min}}\right) \frac{1-\exp[-\alpha(t-t_{min})]}{1-\exp[-\alpha(t_{max}-t_{min})]} \right], \quad (2)$$

where $\alpha \neq 0$ and $y_{min} > 0$, and $y_{max} > 0$. A third form (case III) sets the α parameter to be 0 in the differential equation defining $Y(t)$. This gives

$$Y(t) = \left\{ (y_{min})^{\beta} + \left((y_{max})^{\beta} - (y_{min})^{\beta}\right) \frac{t-t_{min}}{t_{max}-t_{min}} \right\}^{\frac{1}{\beta}}, \quad (3)$$

where $\beta \neq 0$ and $y_{min} > 0$, and $y_{max} > 0$. The fourth form (case IV) sets both α and β parameters to be 0. The resulting 2-parameter model is

$$Y(t) = y_{min} \exp\left[\ln\left(\frac{y_{max}}{y_{min}}\right) \frac{t-t_{min}}{t_{max}-t_{min}} \right], \quad (4)$$

where $y_{min} > 0$ and $y_{max} > 0$.

Two possible error structures were considered for estimating parameters of the Schnute model: additive and multiplicative. The additive error structure consisted of an additive normal term, where, for each data point,

$$y_i = Y(t_i) + \sigma\varepsilon_i, \quad (5)$$

whereas the multiplicative error structure consisted of a lognormally distributed term where, for each data point,

$$y_i = Y(t_i)\exp[\sigma\varepsilon_i]. \quad (6)$$

The random variables ε_i were independent and identically distributed standard normal random variables, and the variance term σ^2 was a positive constant. These two error structures differed in how individual size at age varied about the growth curve. Use of the additive error term implied that the model error in predicting individual size at age was invariant with respect to age. In contrast, the use of a multiplicative error term implied that the model error in predicting individual size at age was scaled with size so that more heterogeneity could be expected in size at age as age increased.

Least-squares estimates of growth parameters under the additive error structure were computed by minimizing the residual sum of squares, R_A, where

$$R_A(y_{min}, y_{max}, \alpha, \beta) = \sum_{i=1}^{n} [y_i - Y(t_i, y_{min}, y_{max}, \alpha, \beta)]^2, \quad (7)$$

Similarly, least-squares estimates of parameters under the multiplicative error structure were computed by minimizing the residual sum of squares R_M, where

$$R_M(y_{min}, y_{max}, \alpha, \beta) = \sum_{i=1}^{n} \left[\ln\left(\frac{y_i}{Y(t_i, y_{min}, y_{max}, \alpha, \beta)} \right) \right]^2. \quad (8)$$

We used SAS to compute least-squares estimates of parameters for the growth models (SAS Institute Inc., 1989). For the additive error structure, the nonlin-

ear regression model was given by Equation 5, whereas for the multiplicative error structure, the nonlinear regression model was

$$z_i = \ln\left(Y(t_i)\right) + \sigma\varepsilon_i, \quad (9)$$

where $z_i = \ln(y_i)$ was the log-transformed size of the i^{th} squid in the data set.

We estimated parameters of the Schnute growth model for several subsets of the length-at-age and weight-at-age data to assess the adequacy of the additive and multiplicative error structures. The goodness of fit of the additive and the multiplicative error structures was compared by testing whether the residuals of estimated growth curves were normally or lognormally distributed with the Shapiro-Wilk test (Shapiro and Wilk, 1965). In particular, parameters for case I of the growth model were estimated for the set of pooled-sex samples (n=353) by using the additive and the multiplicative error structures. The set was then partitioned into immature squid of indeterminate sex (n=76), female (n=131), and male (n=146) samples, and parameters for case I were estimated. We also partitioned the set into samples with hatching dates from June to October (n=145) and from November to May (n=208), and parameters for case I were estimated. Last, female and male samples were partitioned into samples with hatching dates from June to October (n_F=61 and n_M=76) and from November to May (n_F=70 and n_M=70), and parameters of case I were estimated. Overall, growth curves for case I were estimated for each of 10 subsets of the length-at-age and weight-at-age data.

We then estimated parameters for cases II, III, and IV of the Schnute growth model for each of the 10 subsets of size-at-age data using the best error structure. For each subset of size-at-age data, the estimated growth curves were compared on the basis of two criteria. First, an estimated growth curve was rejected if at least one of its parameters was not significantly different from 0 at the 5% level of significance. Second, if more than one growth curve had significant parameters, an analysis of variance of the residual sum of squares (RSS) for full and reduced parameter cases was used to select the best fit on the basis of the variance ratio described by Schnute (1981; see also Bigelow 1994). A comparison between cases II and IV tested whether the hypothesis α=0 was acceptable, and a comparison between cases III and IV tested whether the hypothesis that β=0 was acceptable. Cases II and III were compared on the basis of the lowest RSS. For each of the 10 subsets of data, one growth curve was selected as the best relationship between length at age and weight at age.

Results

Month of hatching

Long-finned squid hatched during all months of the year (Table 2). The fact that some samples hatched during December–April indicated that *L. pealei* were successfully reproducing during the winter. Given this, our data show that *L. pealei* from the northwest Atlantic have the capacity to spawn throughout the year.

The frequency distribution of hatch month of *L. pealei* samples grouped by collection season (Fig. 3) indicated that several microcohorts were present within seasonal collections. For the winter collections (Fig. 3A), most squid were hatched during June–September. Considerable variability in squid size was apparent in the length-frequency distribution (ML ranged from 6.3 to 44.0 cm [μ=19.3, σ=11.1]). Most squid in the spring collections (Fig. 3B) were hatched during August–November. Again, considerable variability in squid size was apparent (ML ranged from 1.8 to 40.8 cm [μ=16.6, σ=9.0]). For the summer collections (Fig. 3C), most of the squid were hatched during December–March, with the exception of 17 juvenile squid of indeterminate sex from the 17 July 1991 Rhode Island Department of Environmental Management survey that hatched during May. In comparison to the winter and spring collections, there was less variability in squid size within the summer collections (ML ranged from 1.3 to 16.3 cm [μ=5.0, σ=3.5]). Most of the squid in the fall collections (Fig. 3D) were hatched during March–May and ML

Table 2

Summary of the number of *Loligo pealei* samples by back-calculated month and year of hatching.

Hatching month	Year			Totals
	1990	1991	1992	
January	—	11	—	11
February	—	10	—	10
March	—	28	17	45
April	—	39	16	55
May	—	39	8	47
June	—	12	4	16
July	4	6	19	29
August	7	7	18	32
September	7	17	6	30
October	18	20	—	38
November	25	6	—	31
December	9	—	—	9
Totals	70	195	88	353

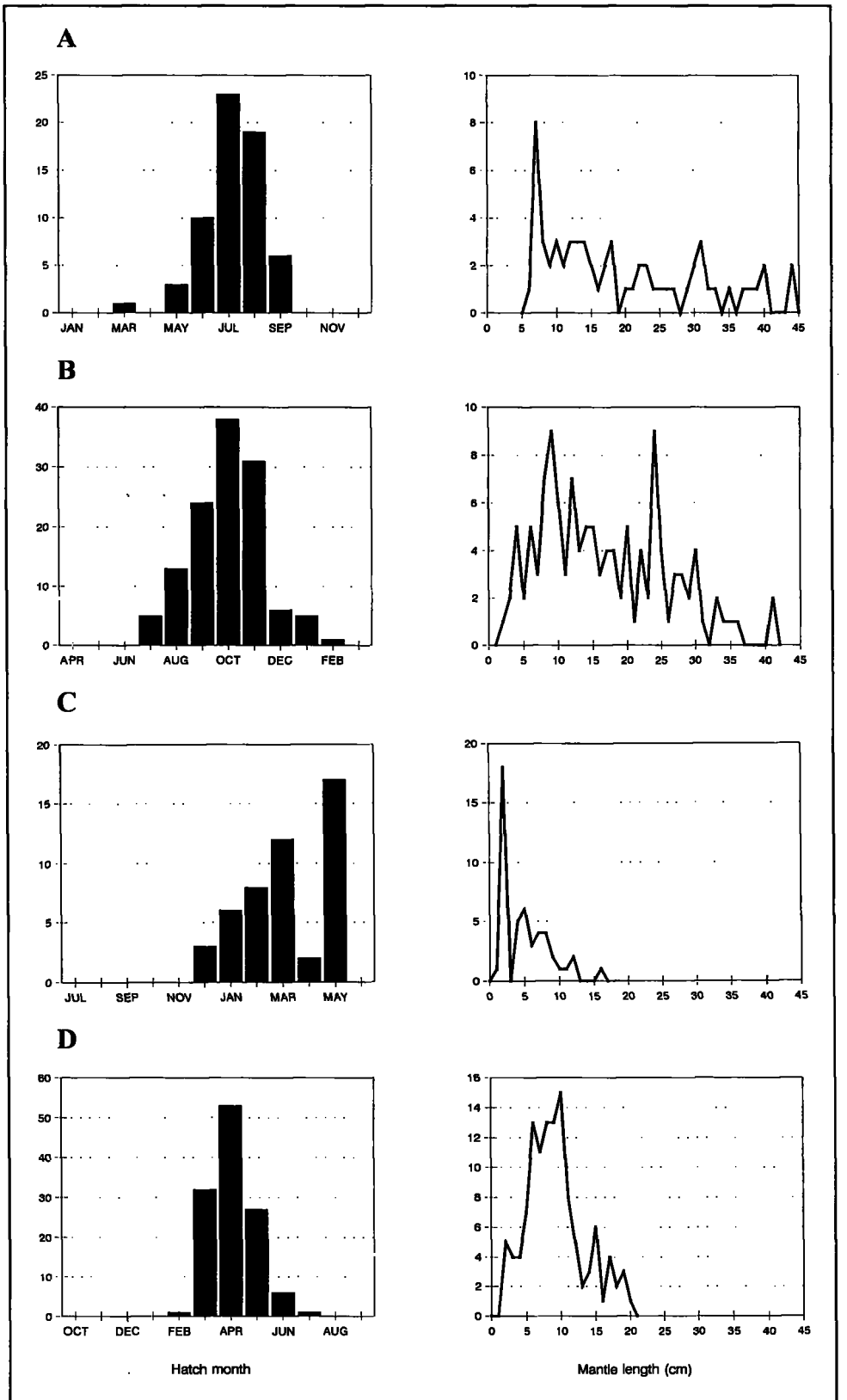

Figure 3

Frequency distributions of hatching month and mantle length of *Loligo pealei* collected during (**A**) winter, (**B**) spring, (**C**) summer, and (**D**) fall.

ranged from 1.8–20.0 cm (μ=9.1, σ=4.1). Squid size in the fall collections was more variable than in the summer collections and less variable than in the winter and spring collections.

Patterns in size at age

The average monthly growth rate in ML and weight suggested that individual growth of *L. pealei* was associated with maturity stage (Table 3) because higher growth rates were apparent for more advanced maturity stages. Relatively large coefficients of variation for the monthly growth rate indicated that the pattern of individual growth was highly variable, especially in terms of weight. Monthly growth rates of indeterminate-sex squid averaged 8.8 mm per month in ML (4.6–15.4 mm/month) and averaged 0.9 g per month in weight (0.1–3.0 g/month). Monthly growth rates of females averaged 18.2 mm per month in ML (8.8–36.6 mm/month) and averaged 9.5 g per month in weight (1.0–40.2 g/month). Monthly growth rates of males averaged 25.9 mm per month in ML (9.6–64.0 mm/month) and averaged 21.4 g per month in weight (1.5–98.2 g/month). The average growth rates in length of females and males were more than twice the average rates for indeterminate-sex squid. Similarly, the average growth rates in weight of females and males were more than 10 times the average rate for indeterminate-sex squid. For males, the average growth rates by length and by weight were 1.4 and 2.2 times greater than for females. Overall, these data indicated that individual growth was highly variable and was related to maturity stage and sex.

Average growth rates were tested for significant differences by sex and maturity stage by using unplanned multiple comparisons procedures. First, squid were categorized as indeterminate-sex, female, or male. With respect to maturity stage, squid were categorized as mature if they were maturing or mature; otherwise they were categorized as immature (Table 2). Bartlett's homogeneity of variance test was then applied to the sex and maturity stage groups. The natural logarithmic transformation was applied to the growth-rate data to stabilize variance prior to testing for differences. The null hypothesis of homogeneous variances for growth rate in length was rejected for the samples grouped by sex (X^2= $40.42>>\chi^2_{0.05[2]}=5.99$) but was accepted for the samples grouped by maturity stage ($X^2=0.40 < \chi^2_{0.05[1]}=3.84$). The null hypothesis of homogeneous variances for growth rate in weight was rejected for the samples grouped by sex ($X^2=9.35>>\chi^2_{0.05[2]}=5.99$) and by maturity stage ($X^2=26.46>>\chi^2_{0.05[1]}=3.84$). Because variances were inherently heteroscedastic and sample sizes were unequal, the unplanned comparison test of Games and Howell (1976) (Day and Quinn, 1989) was applied to test for differences among group means of log-transformed length-at-age data categorized by sex. The group means of indeterminate-sex and female squid ($|Y_I-Y_F|=0.71 > MSD_{0.05[I,F]}=0.14$), indeterminate-sex and male squid ($|Y_I-Y_M|=1.00 > MSD_{0.05[I,M]}=0.16$), and female and male squid ($|Y_F-Y_M|=0.30 > MSD_{0.05[F,M]}=0.16$) were significantly different at the 5% level. For the length-at-age data categorized by maturity stage, the Tukey-Kramer comparison test (Sokal and Rohlf, 1981) was used because variances were homogeneous. The immature

Table 3

Average monthly growth rates and coefficients of variation (CV) in parentheses for long-finned squid, *Loligo pealei*, in length (millimeters per month) and weight (grams per month) and average age (months) by sex and maturity stage.

Sex category and maturity stage	mm per month Average (CV)	g per month Average (CV)	Age (months) Average (CV)	*n*
Indeterminate-sex				
Immature	8.8 (25%)	0.9 (87%)	4.4 (35%)	76
Female				
Immature	15.8 (29%)	5.8 (70%)	6.2 (14%)	88
Maturing	20.0 (24%)	11.3 (73%)	7.0 (16%)	20
Mature	26.1 (21%)	22.1 (44%)	7.5 (13%)	23
Male				
Immature	16.5 (30%)	6.6 (85%)	6.2 (10%)	60
Maturing	21.3 (24%)	12.2 (64%)	6.6 (16%)	15
Mature	34.9 (31%)	35.8 (65%)	7.4 (11%)	71

and mature groups means were significantly different at the 5% level ($|Y_I - Y_M| = 0.78 > MSD_{0.05[I,M]} = 0.08$). Because variances were heteroscedastic for the weight-at-age data grouped by sex and by maturity stage, the Games and Howell test was applied. The group means of indeterminates and females ($|Y_I - Y_F| = 2.47 > MSD_{0.05[I,F]} = 0.46$), indeterminates and males ($|Y_I - Y_M| = 3.08 > MSD_{0.05[I,M]} = 0.50$), and females and males ($|Y_F - Y_M| = 0.62 > MSD_{0.05[F,M]} = 0.40$) were significantly different at the 5% level. Similarly, the immature and mature group means were significantly different at the 5% level ($|Y_I - Y_M| = 2.13 > MSD_{0.05[I,M]} = 0.32$). Overall, the average growth rates in length and weight were found to be significantly different by sex and maturity stage.

The pattern of growth of *L. pealei* analyzed by month of hatching was also highly variable (Table 4). For indeterminate-sex squid, average growth in ML ranged from 5.9 (June-hatched) to 11.2 (September-hatched) mm/month, whereas average growth in weight ranged from 0.2 (July-hatched) to 1.9 (September-hatched) g/month. No seasonal pattern was apparent in the average growth rate for indeterminate-sex squid. However, few samples of indeterminate-sex squid hatched during July to December were available, and comparisons of growth rate by season of hatching were not possible. For females, average growth in ML ranged from 11.1 (December-hatched) to 22.5 (October-hatched) mm/month whereas average growth in weight ranged from 2.2 (December-hatched) to 19.5 (June-hatched) g/month. Average growth rates were generally higher for squid hatched from June to October when the average growth rate in weight exceeded 10 g/month. For males, average growth in ML ranged from 13.9 (December-hatched) to 40.9 (June-hatched) mm/month whereas growth in weight ranged from 3.4 (December-hatched) to 53.3 (June-hatched) g/month. Average growth rates of males were generally highest for squid hatched from June to October when the average growth rate in weight exceeded 20 g/month. Overall, these data suggested that the highest average growth rates were achieved by adult squid hatched from June to October.

The average growth rates by hatch month were also tested for significant differences by using unplanned multiple-comparisons procedures where the natural logarithmic transformation was applied to stabilize variance. The null hypothesis of homogeneous variances for the samples grouped by hatch month was rejected for growth in length ($X^2 = 44.41 >> \chi^2_{0.05[11]} = 19.67$) and in weight ($X^2 = 75.71 >> \chi^2_{0.05[11]} = 19.67$). A total of 16 pairs of group means for growth rate in length were significantly different at the 5% level (Table 5): July–January; July–February; July–March; July–April; July–May; July–November; July–December; September–April; September–May; September–December; October–January; October–March; October–April; October–May; October–November; and October–December. Overall, these tests indicated that there were significant differences between growth rates of squid hatched during November–May and July–October. Similarly, for growth rate in weight, a total of 16 pairs of group means for growth rate in length were significantly different at the 5% level (Table 6): July–January; July–February; July–March; July–April; July–May; July–November; July–December; August–May; September–April; September–May; September–December; October–March; October–April; October–May; October–November; and October–December. Overall, these tests indicated that there were significant differences between growth rates of squid hatched during November–May and July–October.

There was no consistent pattern in growth of *L. pealei* analyzed by year of hatching (Table 7). For indeterminate-sex squid, average growth in ML was lowest in 1990 (8.5 mm/month) and highest in 1992 (12.3 mm/month), whereas average growth in weight was lowest in 1991 (0.7 g/month) and highest in 1992 (2.2 g/month). For females, average growth in ML and weight was lowest in 1992 (16.3 mm/month and 7.2 g/month) and highest in 1990 (21.5 mm/month and 15.2 g/month). For males, average growth in ML and weight was lowest in 1992 (21.9 mm/month and 13.2 g/month) and highest in 1991 (27.8 mm/month and 25.0 g/month). Overall, these data suggested that growth rates varied by sex among years.

The average growth rates by hatch year were also tested for significant differences by using unplanned multiple-comparisons procedures where the natural logarithmic transformation was applied to stabilize variance. The null hypothesis of homogeneous variances for the samples grouped by hatch year was rejected for growth in length ($X^2 = 26.12 >> \chi^2_{0.05[2]} = 5.99$) and weight ($X^2 = 47.90 >> \chi^2_{0.05[2]} = 5.99$). The group means of 1990 and 1991 hatched squid were significantly different in length ($|Y_{1990} - Y_{1991}| = 0.28 > MSD_{0.05[1990,1991]} = 0.26$) and weight ($|Y_{1990} - Y_{1991}| = 0.93 > MSD_{0.05[1990,1991]} = 0.67$), but no general trend in growth by year was apparent.

Growth model

The additive and the multiplicative error structures were compared by testing whether the residuals of estimated case-I growth curves were normally or log-normally distributed. For 8 out of 10 subsets of length-at-age data, the hypothesis of an additive normal error structure was rejected at the 5% level. In contrast, the hypothesis of a multiplicative log-

Table 4

Average monthly growth rates and coefficients of variation (CV) for long-finned squid, *Loligo pealei,* in length (millimeters per month) and weight (grams per month) and average age (months) by sex and month of hatching.

Sex category and hatching months	mm per month Average (CV)	g per month Average (CV)	Age (months) Average (CV)	*n*
Indeterminate-sex				
January	8.3 (27%)	0.6 (58%)	4.2 (9%)	5
February	9.6 (16%)	1.1 (57%)	4.7 (11%)	7
March	10.6 (13%)	1.4 (29%)	5.1 (27%)	10
April	8.7 (24%)	1.1 (71%)	5.6 (22%)	15
May	8.8 (26%)	0.6 (141%)	3.0 (45%)	25
June	5.9 (18%)	0.3 (43%)	4.0 (6%)	6
July	6.1	0.2	3.4	1
September	11.2	1.9	6.2	1
November	8.7 (9%)	1.3 (29%)	6.1 (2%)	3
December	8.4 (23%)	0.9 (74%)	5.3 (3%)	3
Female				
January	13.2 (9%)	3.2 (27%)	6.0 (6%)	4
March	15.7 (25%)	5.6 (80%)	5.9 (21%)	16
April	17.2 (33%)	6.7 (68%)	5.8 (6%)	25
May	18.4 (30%)	8.0 (100%)	5.4 (19%)	12
June	19.5 (75%)	19.5 (128%)	7.7 (6%)	2
July	21.2 (21%)	15.9 (66%)	7.8 (8%)	9
August	17.9 (32%)	10.9 (78%)	7.4 (10%)	15
September	19.4 (32%)	11.4 (70%)	7.2 (12%)	17
October	22.5 (31%)	14.7 (74%)	6.9 (6%)	18
November	15.7 (43%)	6.3 (130%)	6.3 (3%)	12
December	11.1	2.2	6.7	1
Male				
January	19.6 (46%)	9.1 (100%)	6.0 (7%)	2
February	20.5 (22%)	8.2 (12%)	6.1 (22%)	3
March	20.8 (30%)	13.0 (74%)	6.8 (14%)	19
April	17.1 (28%)	6.9 (79%)	5.9 (5%)	15
May	21.9 (55%)	15.6 (141%)	5.7 (18%)	10
June	40.9 (19%)	53.3 (37%)	7.8 (11%)	8
July	35.5 (36%)	41.8 (66%)	7.6 (7%)	19
August	27.9 (53%)	25.4 (105%)	7.4 (12%)	17
September	33.1 (27%)	29.4 (47%)	7.5 (9%)	12
October	29.6 (36%)	21.1 (62%)	6.9 (5%)	20
November	17.4 (46%)	7.8 (157%)	6.1 (5%)	16
December	13.9 (16%)	3.4 (43%)	5.9 (12%)	5
Pooled-sex				
January	12.1 (45%)	3.1 (140%)	5.2 (19%)	11
February	12.8 (45%)	3.2 (108%)	5.1 (20%)	10
March	16.8 (37%)	7.8 (106%)	6.1 (21%)	45
April	14.9 (40%)	5.2 (93%)	5.8 (12%)	55
May	14.0 (61%)	5.6 (215%)	4.2 (42%)	47
June	25.1 (72%)	29.2 (101%)	6.4 (31%)	16
July	30.1 (44%)	32.3 (82%)	7.5 (13%)	29
August	23.2 (53%)	18.6 (115%)	7.4 (11%)	32
September	24.6 (41%)	18.3 (77%)	7.3 (11%)	30
October	26.2 (37%)	18.1 (68%)	6.9 (5%)	38
November	16.0 (47%)	6.6 (154%)	6.2 (4%)	31
December	11.8 (28%)	2.5 (66%)	5.8 (12%)	9

normal error structure could not be rejected for any subset of the length-at-age data. Similarly, for all 10 subsets of weight-at-age data, the hypothesis of an additive normal error structure was rejected at the 5% level, whereas the hypothesis of a multiplicative lognormal error structure could not be rejected for any subset. As a result, the multiplicative error structure was considered to be the best assumption for modelling variability in size at age.

Although the residuals from the curves estimated with the multiplicative error structure conformed to model assumptions, the parameters of these curves were imprecisely determined. In particular, the case-I curve was rejected for each subset of length-at-age and weight-at-age data because there was at least one parameter that was not significantly different from 0. Thus, the 4-parameter form of the Schnute model had more parameters than necessary to characterize *L. pealei* growth.

For the length-at-age growth curves, most of the case-II and case-III curves were rejected because their parameters were not significant. As a result, there were only 3 instances where comparison of RSS was used to select the best curve. The best curve for pooled-sex samples hatched during June–October was the case-II curve which was selected over the case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=14.98 > 3.91=F_{0.05}(1,142)$). The best curve

Table 5

Results of Games and Howell test of differences between means of log-transformed growth rate in length by hatch month of long-finned squid, *Loligo pealei*. Absolute values of differences between means are given below the diagonal and corresponding values of the maximum significant difference at the 5% level are given above the diagonal. Significantly different means are indicated with an asterisk.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	—	0.94	0.77	0.77	0.78	1.41	0.81	0.80	0.80	0.77	0.77	0.86
Feb	0.06	—	0.77	0.77	0.79	1.41	0.81	0.80	0.80	0.77	0.77	0.86
Mar	0.34	0.28	—	0.37	0.44	1.32	0.52	0.49	0.47	0.39	0.40	0.63
Apr	0.21	0.15	0.13	—	0.44	1.32	0.52	0.49	0.48	0.39	0.41	0.63
May	0.09	0.03	0.25	0.12	—	1.33	0.56	0.54	0.53	0.46	0.47	0.65
Jun	0.45	0.39	0.11	0.24	0.36	—	1.34	1.34	1.33	1.32	1.32	1.36
Jul	**0.89***	**0.83***	**0.55***	**0.68***	**0.80***	0.44	—	0.60	0.60	0.53	0.55	0.70
Aug	0.62	0.56	0.28	0.41	0.53	0.17	0.27	—	0.56	0.51	0.52	0.68
Sep	0.70	0.64	0.36	**0.49***	**0.61***	0.25	0.19	0.08	—	0.50	0.51	0.67
Oct	**0.79***	0.73	**0.45***	**0.58***	**0.70***	0.34	0.10	0.17	0.09	—	0.43	0.64
Nov	0.28	0.22	0.06	0.08	0.19	0.16	**0.60***	0.33	0.41	**0.50***	—	0.64
Dec	0.01	0.05	0.33	0.19	0.08	0.43	**0.87***	0.60	**0.68***	**0.77***	0.27	—

Table 6

Results of Games and Howell test of differences between means of log-transformed growth rate in weight by hatch month for long-finned squid, *Loligo pealei*. Absolute values of differences between means are given below the diagonal and corresponding values of the maximum significant difference at the 5% level are given above the diagonal. Significantly different means are indicated with an asterisk.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	—	2.85	2.38	2.41	2.52	3.94	2.47	2.42	2.42	2.37	2.41	2.61
Feb	0.18	—	2.23	2.22	2.37	3.85	2.31	2.28	2.27	2.21	2.22	2.48
Mar	1.14	0.96	—	1.02	1.49	3.53	1.33	1.20	1.19	0.94	1.02	1.78
Apr	0.78	0.60	0.36	—	1.48	3.53	1.32	1.18	1.17	0.93	1.00	1.80
May	0.21	0.39	1.35	1.00	—	3.62	1.69	1.61	1.60	1.43	1.48	2.00
Jun	1.32	1.14	0.18	0.54	1.53	—	3.59	3.57	3.56	3.50	3.53	3.65
Jul	**2.61***	**2.43***	**1.47***	**1.83***	**2.83***	1.30	—	1.47	1.46	1.26	1.32	1.90
Aug	1.94	1.76	0.80	1.16	**2.16***	0.62	0.67	—	1.33	1.14	1.21	1.85
Sep	2.07	1.89	0.93	**1.29***	**2.29***	0.75	0.54	0.13	—	1.13	1.20	1.84
Oct	2.22	2.04	**1.08***	**1.44***	**2.44***	0.90	0.39	0.28	0.15	—	0.93	1.77
Nov	1.02	0.84	0.12	0.24	1.23	0.30	**1.59***	0.92	1.05	**1.20***	—	1.80
Dec	0.23	0.05	0.91	0.56	0.44	1.09	**2.39***	1.72	**1.85***	**1.99***	0.79	—

Table 7

Average monthly growth rates and coefficients of variation (CV) for long-finned squid, *Loligo pealei*, in length (millimeters per month), weight (grams per month), and average age (months) by sex and year of hatching.

Sex category and hatching year	mm per month Average (CV)	g per month Average (CV)	Age (months) Average (CV)	*n*
Indeterminate-sex				
1990	8.5 (16%)	1.1 (48%)	5.7 (8%)	6
1991	8.5 (23%)	0.7 (89%)	4.2 (37%)	65
1992	12.3 (17%)	2.2 (20%)	5.4 (17%)	5
Totals	8.8 (25%)	0.9 (87%)	4.4 (35%)	76
Female				
1990	21.5 (42%)	15.2 (87%)	6.7 (10%)	24
1991	18.4 (27%)	9.0 (72%)	6.5 (19%)	61
1992	16.3 (31%)	7.2 (95%)	6.5 (14%)	46
Totals	18.2 (34%)	9.5 (91%)	6.5 (16%)	131
Male				
1990	27.5 (47%)	22.7 (89%)	6.9 (13%)	40
1991	27.8 (46%)	25.0 (102%)	6.8 (16%)	69
1992	21.9 (40%)	13.2 (94%)	6.7 (12%)	37
Totals	25.9 (47%)	21.4 (102%)	6.8 (14%)	146
Pooled-sex				
1990	23.8 (52%)	18.3 (100%)	6.8 (13%)	70
1991	18.4 (62%)	11.9 (156%)	5.8 (30%)	195
1992	18.0 (39%)	9.4 (106%)	6.6 (14%)	88
Totals	19.4 (56%)	12.5 (136%)	6.2 (24%)	353

for female samples hatched during November–May was the case-IV curve which was selected over the case-II curve because the hypothesis α=0 was accepted (f=2.68 < 3.98=$F_{0.05}$(1,67)). The best curve for male samples hatched during June–October was the case-II curve which was selected over the case-IV curve because the hypothesis α=0 was rejected (f=5.46 > 3.97=$F_{0.05}$(1,73)). For each of the 7 other subsets of length-at-age data, case IV yielded the best growth curve (Table 8).

Case-IV curves were the best growth models for length at age of pooled-sex samples (Fig. 4A) and pooled-sex samples hatched during November–May (Fig. 5A). In general, the case-IV growth curves are power functions that represent unbounded accelerating growth with a theoretical minimum size. In particular, case-IV curves are what Schnute termed "T^{th} power" growth curves, where size (G) at age (T) is proportional to some positive constant K>1 raised to the T^{th} power. That is, $G \propto K^T = \exp[T \ln(K)]$, so that size increases exponentially as age increases. In contrast, the case-II curve was chosen for pooled-sex samples hatched during June–October (Fig. 5A). For these samples, growth in length appeared nearly linear over the range of data, although there was some indication of a slight decrease in growth rate past 250 days of age.

For the length-at-age data partitioned by sex, case-IV curves were also the best growth models, with one exception. Exponential growth in length was evident for indeterminate-sex (Fig. 6A), female (Fig. 7A), and male (Fig. 7A) samples. Similarly, growth in length was exponential for female samples hatched during June–October and during November–May (Fig. 8A) and for male samples hatched during November–May (Fig. 9A). In contrast, growth in length for males hatched during June–October was not exponential (Fig. 9A) and growth rate decreased between 200 and 250 days of age.

For the subsets of the weight-at-age growth data, most of the case-II and case-III curves were rejected because their parameters were not significant and there were only 4 instances where comparison of RSS was used to select the best curve. The best curve for pooled-sex samples was the case II curve which was selected over the case-IV curve because the hypothesis α=0 was rejected (f=4.30 > 3.87=$F_{0.05}$(1,350)). The best curve for indeterminate-sex samples was the case-II curve which was selected over case-IV curve because the hypothesis α=0 was rejected (f=5.61 >

Table 8

Summary of best growth curves for long-finned squid, *Loligo pealei*, length (cm) at age (months).

Data set	Sample size	Growth curve	r^2	α	β	t_{min}	y_{min}	t_{max}	y_{max}
Pooled-sex samples	353	IV	0.97	—	—	1.6427	1.3670	9.7249	47.1939
Indeterminate-sex samples	76	IV	0.97	—	—	1.6427	1.5267	6.8993	7.3841
Female samples	131	IV	0.98	—	—	4.0739	6.1918	9.2320	21.2922
Male samples	146	IV	0.98	—	—	4.4353	5.4317	9.7249	57.8786
Pooled-sex samples hatched Jun–Oct	145	II	0.98	0.2867	—	3.4497	1.4801	9.2320	30.6814
Pooled-sex samples hatched Nov–May	208	IV	0.97	—	—	1.6427	1.5796	9.7249	37.4441
Female samples hatched Jun–Oct	61	IV	0.99	—	—	5.4209	8.8066	9.2320	22.5526
Female samples hatched Nov–May	70	IV	0.98	—	—	4.0739	6.9978	8.6078	13.8768
Male samples hatched Jun–Oct	76	II	0.99	0.8284	—	5.6509	6.1309	9.1335	32.5621
Male samples hatched Nov–May	70	IV	0.98	—	—	4.4353	5.9896	9.7249	36.6641

$3.97=F_{0.05}(1,74)$). The best curve for pooled-sex samples hatched during June–October was the case-II curve which was selected over the case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=18.64 > 3.91=F_{0.05}(1,142)$). The best curve for pooled-sex samples hatched during November–May was the case-III curve which was selected over case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=6.82 > 3.89=F_{0.05}(1,205)$). For each of the 6 other subsets of length-at-age data, case IV yielded the best growth curve (Table 9).

For the weight-at-age data, case-II growth curves were chosen for pooled-sex samples (Fig. 4B) and pooled-sex samples hatched during June–October (Fig. 5B). Although these curves are sigmoidal and eventually approach an asymptote (cf. Schnute, 1981), it is important to note that the asymptotes are not approached within the range of data for the estimated curves and that growth is nearly exponential for the observed ages. In contrast, a case-III growth curve was chosen for pooled-sex samples hatched during November–May (Fig. 5B). This growth curve is not asymptotic and consists of an initial period of decelerated growth followed by a period of accelerated growth after a certain size is reached.

Case-IV growth curves were chosen for every data set where the weight-at-age data were partitioned by sex, with one exception. Growth in weight was exponential for female and male samples (Fig. 7B). Similarly, exponential growth was evident for female samples hatched during June–October and during November–May (Fig. 8B) and for male samples hatched during June–October and during November–May (Fig. 9B). In contrast, a case-II curve was chosen for indeterminate-sex squid (Fig. 6B), although growth rate was effectively exponential for the observed ages. In this case, the estimated curve would approach an asymptote outside the range of possible sizes for *L. pealei* that lack identifiable sexual characteristics.

For adult squid, the estimated growth curves indicated sexual dimorphism. Length-at-age curves for female (L_F) and male (L_M) samples were

$$\begin{aligned} L_F(d) &= 2.3343e^{0.0079d} \\ L_M(d) &= 0.7470e^{0.0147d}, \end{aligned} \tag{10}$$

where L is mantle length in centimeters and age (d) is measured in days (Fig. 7A). Similarly, weight-at-age curves for female (W_F) and male (W_M) samples were

$$\begin{aligned} W_F(d) &= 1.1446e^{0.0182d} \\ W_M(d) &= 0.1316e^{0.0311d}, \end{aligned} \tag{11}$$

Table 9

Summary of best growth curves for long-finned squid, *Loligo pealei*, weight (g) at age (months).

Data set	Sample size	Growth curve	r^2	α	β	t_{min}	y_{min}	t_{max}	y_{max}
Pooled-sex samples	353	II	0.94	0.0577	—	1.6427	0.1813	9.7249	783.6477
Indeterminate-sex samples	76	II	0.85	0.2058	—	1.6427	0.1985	6.8993	11.2208
Female samples	131	IV	0.96	—	—	4.0739	10.9940	9.2320	192.8125
Male samples	146	IV	0.97	—	—	4.4353	8.7765	9.7249	1314.8945
Pooled-sex samples hatched Jun–Oct	145	II	0.96	0.3038	—	3.4497	0.3545	9.2320	365.0887
Pooled-sex samples hatched Nov–May	208	III	0.92	—	0.1315	1.6427	0.1820	9.7249	323.5635
Female samples hatched Jun–Oct	61	IV	0.97	—	—	5.4209	23.7236	9.2320	222.6014
Female samples hatched Nov–May	70	IV	0.96	—	—	4.0739	14.1734	8.6078	78.0026
Male samples hatched Jun–Oct	76	IV	0.97	—	—	5.6509	39.6333	9.1335	681.9745
Male Samples hatched Nov–May	70	IV	0.97	—	—	4.4353	10.1822	9.7249	633.1753

where weight (W) is in grams and age (d) is measured in days (Fig. 7B). These curves gave instantaneous daily growth rates of 0.8% and 1.5% in length and of 1.8% and 3.1% in weight for females and males, respectively. Thus, female growth in length and weight was generally slower than that for males.

The estimated growth curves also indicated differences in growth rate between hatching seasons for both sexes. Length-at-age curves for female squid hatched during June–October ($L_{F,JO}$) and female squid hatched during November–May ($L_{F,NM}$) were (Fig. 8A):

$$L_{F,JO}(d) = 2.3116e^{0.0081d}$$
$$L_{F,NM}(d) = 3.7828e^{0.0050d}. \quad (12)$$

Weight-at-age curves for female squid hatched during June–October ($W_{F,JO}$) and female squid hatched during November–May ($W_{F,NM}$) were (Fig. 8B):

$$W_{F,JO}(d) = 0.9820e^{0.0193d}$$
$$W_{F,NM}(d) = 3.0617e^{0.0124d}. \quad (13)$$

These curves gave instantaneous daily growth rates of 0.8% and 0.5% in length and of 1.9% and 1.2% in weight for females hatched during June–October and during November–May, respectively. Thus, female growth rate in length and weight was generally more rapid for June–October hatched squid.

Differences in growth rate between hatching seasons were also evident for male squid. In particular, male growth in length (Fig. 9A) was more rapid at younger ages (≤225 d) for June–October hatched squid than for November–May hatched squid. In contrast, male growth in length was estimated to be more rapid at older ages (>225 d) for November–May hatched squid than for June–October hatched squid (Fig. 9A). However, this comparison should be viewed with caution because the sample size of older males hatched during November–May available for estimating the length-at-age curve was small. Weight-at-age curves (Fig. 9B) for male squid hatched during June–October ($W_{M,JO}$) and male squid hatched during November–May ($W_{M,NM}$) were

$$W_{M,JO}(d) = 0.3917e^{0.0268d}$$
$$W_{M,NM}(d) = 0.3190e^{0.0256d}. \quad (14)$$

These curves gave instantaneous daily growth rates of 2.7% and 2.6% of body weight for males hatched

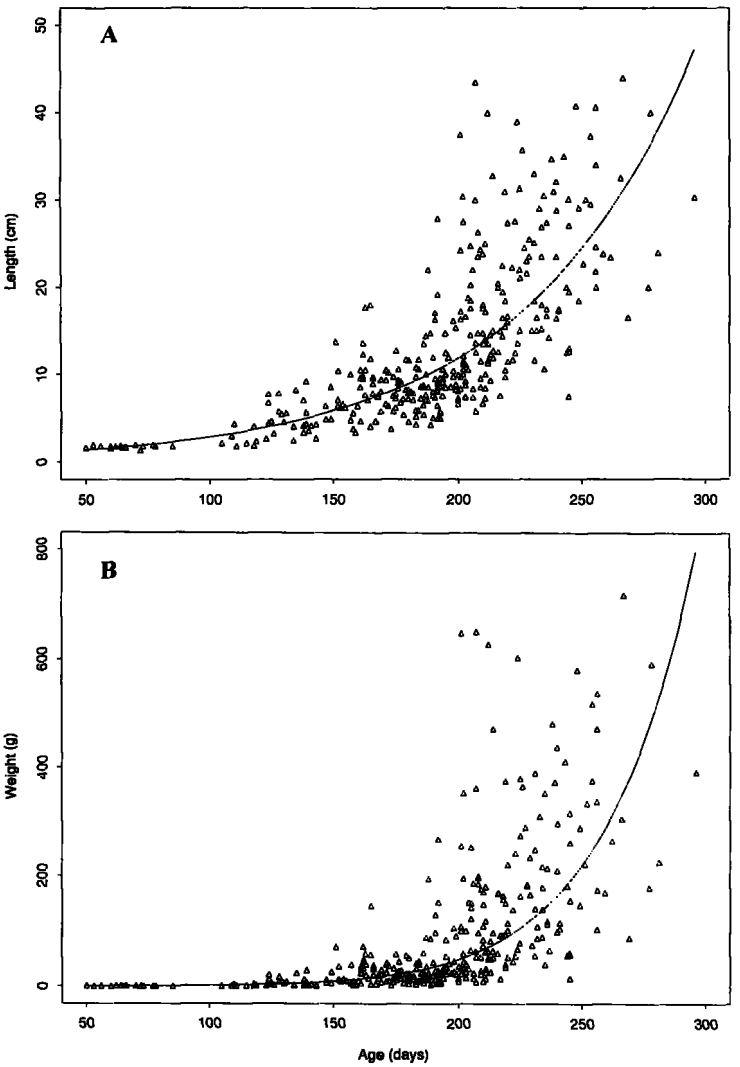

Figure 4

Growth curves for pooled-sex *Loligo pealei* in length (**A**) and in weight (**B**).

during June–October and during November–May, respectively. Overall, female growth in length and weight and male growth in weight were more rapid for June–October hatched squid. Male growth in length was also more rapid at younger ages for squid hatched during June–October than for squid hatched during November–May.

The selected growth curves indicated that *L. pealei* growth was dependent upon maturity stage, sex, and hatching season. Indeterminate-sex squid grew more slowly than adults whereas males grew more rapidly than females. Further, squid hatched during June–October grew more rapidly than squid hatched during November–May.

Discussion

Growth rates obtained in this study were generally higher than those reported in Hixon et al. (1981, Tables 1 and 2) but were lower than those in studies of cultured *L. pealei*. In particular, average monthly growth rates for males reported in this study (26 mm/month and 21 g/month) were lower than those reported by Hanlon et al. (1983) who found average growth rates of 44 mm/month and 37 g/month in a sample of 6 male *L. pealei* raised in a closed sea-water system. Additionally, Hanlon et al. (1987) reported an instantaneous daily growth rate of roughly 2% in ML for 10 *L. pealei* raised in a closed sea-water sys-

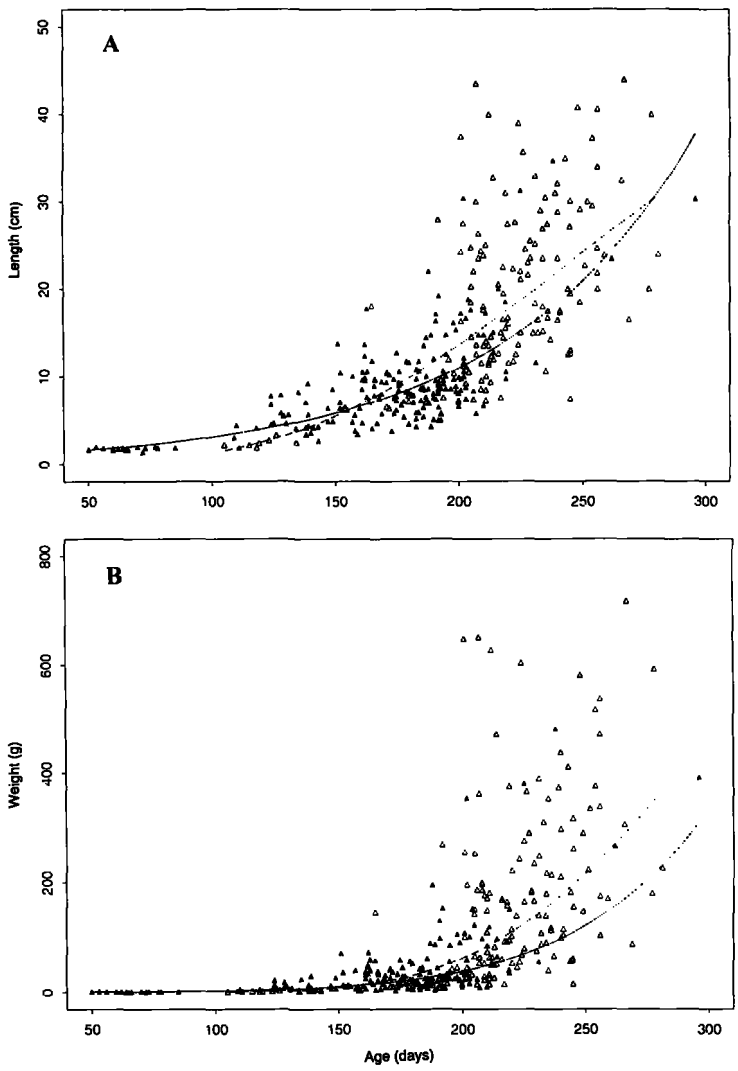

Figure 5

Growth curves for pooled-sex *Loligo pealei* hatched during June–October (dashed line and open triangles) and during November–May (solid line and solid triangles) in length (**A**) and in weight (**B**).

tem whereas the estimated growth curve for pooled-sex samples in this study indicated a growth rate of 1.4%. While the lower growth rates of wild squid were likely due to the better growth conditions experienced by the cultured squid, it should be noted that the largest squid in this study, a 44-cm male, was only 2.5 cm smaller than the largest reported *L. pealei*[5] (Summers, 1968). The fact that this 9-month-old male could have achieved the maximum reported size if it grew for one more month at average male growth rate suggested that it was unlikely that the lifespan of *L. pealei* exceeded 1 year.

Although a comprehensive growth model for squid has not yet been determined (Jackson, 1994a), we suggest that the Schnute model is a viable choice given its flexibility. In addition, we recommend the methods used to select the best form of the growth model because they provide an objective basis for evaluating alternative forms. Even though there was substantial heterogeneity in *L. pealei* size at age, the estimated growth curves for pooled sexes indicated that *L. pealei* growth in length and weight was effec-

[5] Based on a total of 55,616 length-frequency measurements, the maximum size of *L. pealei* taken in the domestic commercial fishery during 1972–91 was 45 cm (Northeast Fisheries Science Center, Woods Hole, MA, unpubl. data).

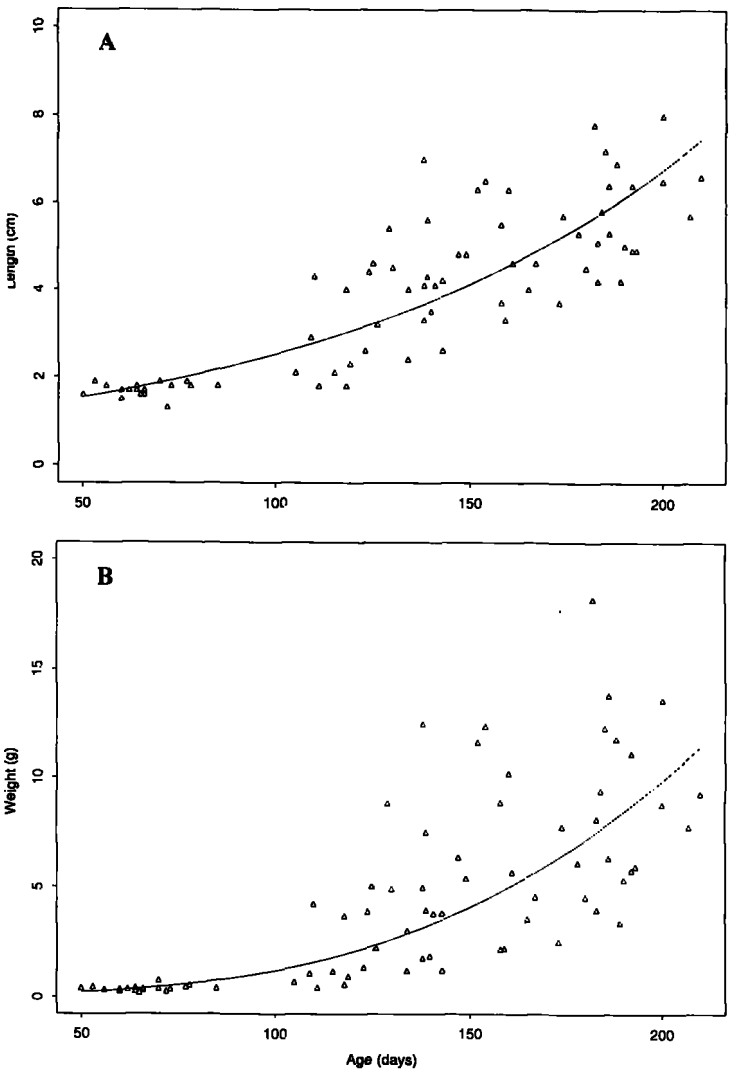

Figure 6

Growth curves of indeterminate-sex *Loligo pealei* in length (**A**) and in weight (**B**).

tively exponential, which is consistent with the findings of Forsythe and Van Heukelem (1987).

It is important to account for individual heterogeneity in size at age when determining a growth curve because the use of mean values for size classes can obscure the pattern of individual growth (Alford and Jackson, 1993). In this study, growth curves were estimated by using size-at-age data for individual squid. We found that the use of a multiplicative lognormal error term provided an adequate statistical framework for estimating growth curves despite substantial heterogeneity in squid size at age. In general, a growth curve with a multiplicative lognormal error term will be more appropriate than an additive normal error term when size-at-age distributions are skewed because prediction error scales with size at age under the lognormal assumption. Regardless, it is recommended that researchers use residual patterns to evaluate the adequacy of an assumed error structure for estimating a growth curve.

The fact that some *L. pealei* were hatched during December–April was unexpected because the protracted spawning season of *L. pealei* in the northwest Atlantic had previously been considered to extend from roughly April to November (Lange, 1982). McMahon and Summers (1971) found that embryonic development of *L. pealei* was related to water temperature. In their study, the average development time required before hatching was 26.7 days for wa-

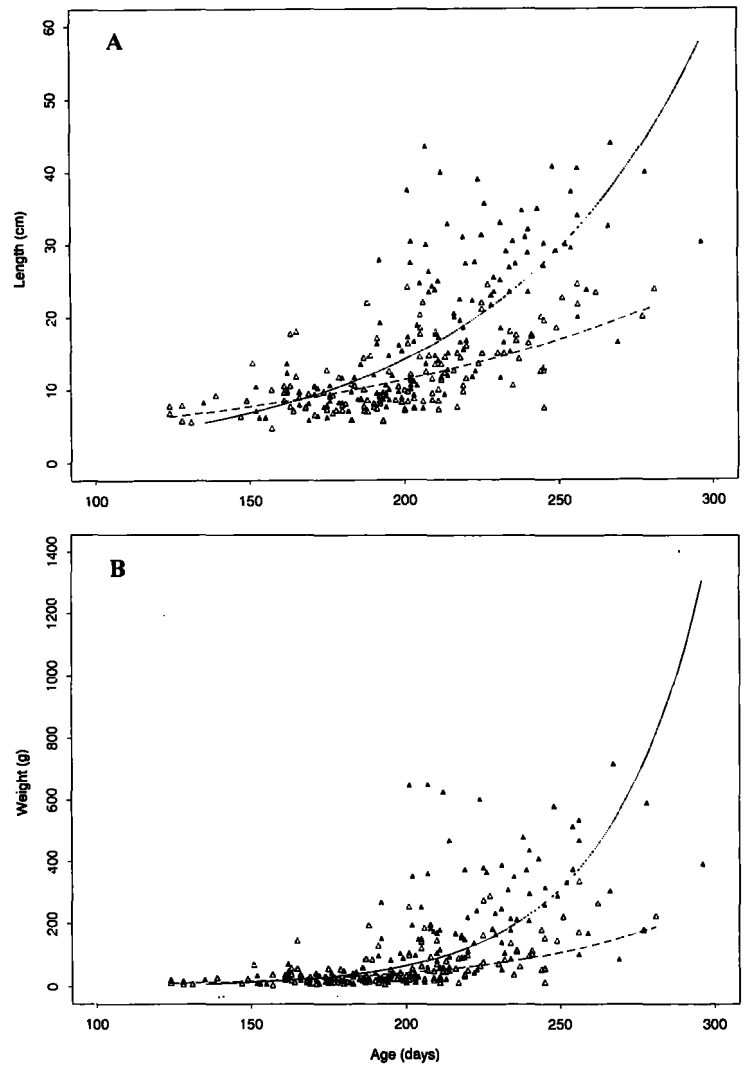

Figure 7

Growth curves for female (dashed line and open triangles) and male (solid line and solid triangles) *Loligo pealei* in length (**A**) and in weight (**B**).

ter temperatures of 12.0–18.0°C, 18.5 days for water temperatures of 15.5–21.3°C, and 10.7 days for water temperatures of 21.5–23.0°C. During winter, *L. pealei* move offshore to the edge of the continental shelf to avoid cooler inshore waters (Lange, 1982). Assuming that squid hatched during December–April encountered water temperatures of 9.0–13.0°C that are characteristic of the convergence zone at the edge of the continental shelf (Bowman, 1977), it would have taken about 1 month for them to develop to the hatching stage. Although our results indicated that winter spawning occurred, further research will be needed to evaluate the relative contribution of winter-hatched squid to the population's dynamics.

Our results lend support to the hypothesis that growth of *L. pealei* can be influenced by seasonal environmental variation and month of hatching. Empirical differences in growth rates between June–October and November–May hatched squid were apparent for both females and males. Further, significant differences in growth rate were detected between squid hatched during November–May and July–October. These differences were also evident in estimated growth curves. The notion that *L. pealei* growth can be influenced by hatching season and its associated temperature regime is consistent with the results of Rodhouse and Hatfield (1990b) who found an apparent effect of seasonal environmental varia-

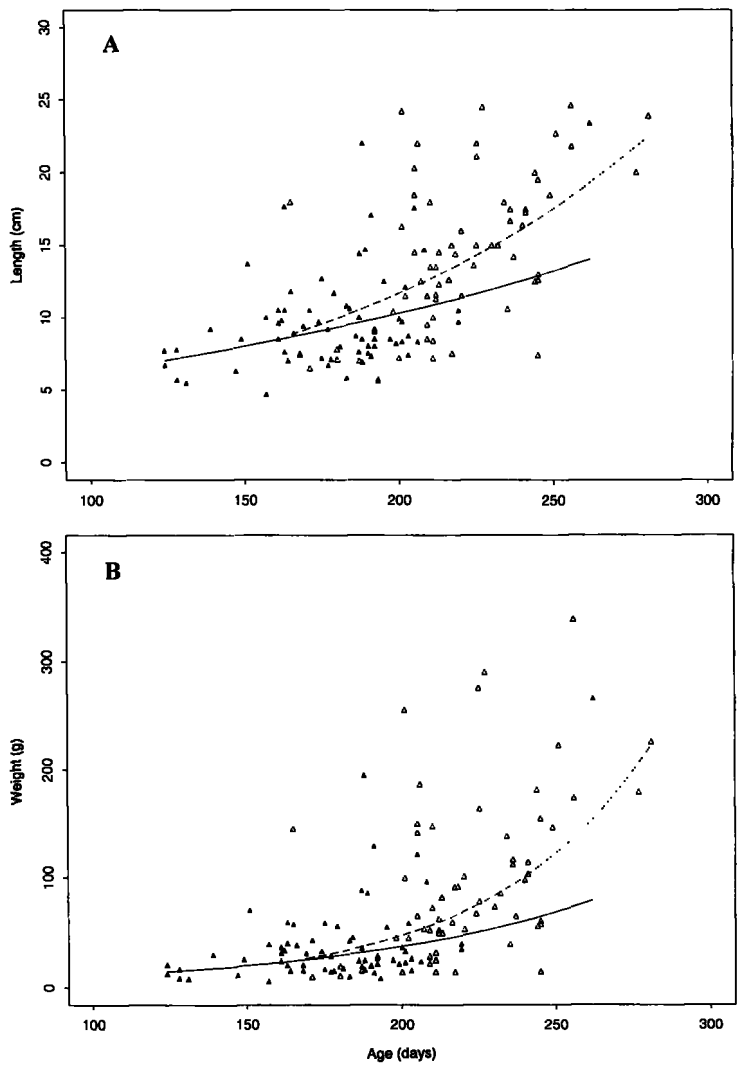

Figure 8

Growth curves for female *Loligo pealei* hatched during June–October (dashed line and open triangles) and during November–May (solid line and solid triangles) in length (**A**) and in weight (**B**).

tion on the growth rate of the Argentine short-finned squid, *Illex argentinus*. Using statolith ageing techniques, they found that older short-finned squid hatched during cooler months apparently grew more slowly than younger squid hatched during warmer months. They speculated that the faster growth of the younger cohort was due to the generally warmer temperatures experienced by hatchlings. Similarly, Forsythe (1993) conducted a simulation study to examine the potential effects of seasonal temperature regimes on the growth of juvenile cephalopods. He showed that small temperature changes could have a substantial effect on the growth of juvenile squid under certain conditions. Overall, further research to estimate directly the potential effect of temperature on the growth rate of *L. pealei* would help to quantify the potential yield from this resource on a seasonal basis.

The fact that the growth rate of *L. pealei* was found to be associated with maturity stage also has potential implications for the management of the resource. Empirical differences in growth rate by maturity stage were consistent for both females and males; on average, growth rates in length and weight were lowest for immature squid and highest for mature squid. Significant differences in growth rate by length

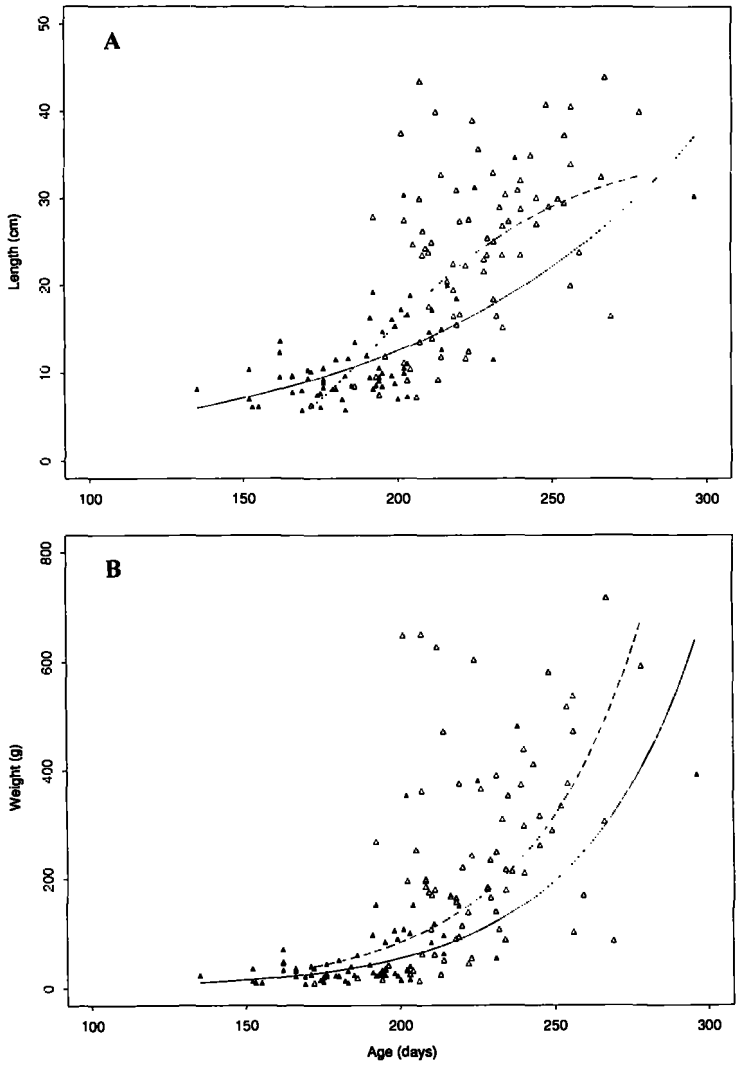

Figure 9

Growth curves for male *Loligo pealei* hatched during June–October (dashed line and open triangles) and during November–May (solid line and solid triangles) in length (**A**) and in weight (**B**).

and weight were also detected between immature and mature squid. In general, intensive harvest of slow-growing immature squid has the potential to reduce fishery production through a decrease in yield per recruit.

No clear effect of hatch year on growth rate was detected in this study. However, these data were not collected for the purpose of examining yearly differences in growth rates, and any annual effects were likely confounded by the effects of hatch month, sex, and maturity stage. Further research conducted with more extensive multi-year collections will likely be needed to ascertain the importance of annual effects on growth rate.

The estimated growth curves for indeterminate-sex squid indicated that their pattern of growth was exponential as suggested by Hanlon et al. (1987) who examined growth rates of juvenile *L. pealei* in closed-system aquaria. Growth of indeterminate-sex squid in weight was less rapid than that for adults and would be predicted to slow outside the range of observed ages, when these juveniles would develop identifiable sexual characteristics. In contrast, growth of indeterminate-sex squid in length was roughly 1.0% per day. In comparison, growth curves for females and males indicated exponential growth with instantaneous daily growth rates of 0.8% to 1.5%

in ML and 1.8% to 3.1% in weight. The exponential growth of *L. pealei* throughout their life cycle is consistent with the fact that squid have high gross-growth efficiency and are metabolic maximizers in comparison with teleosts (O'Dor and Webber, 1986).

The difference between growth rate in weight of indeterminate-sex squid and adults suggests that there may be a body size above which growth rate increases substantially. This critical size could be related to changes in diet because *L. pealei* undergo an ontogenetic shift in prey selection from crustaceans to fish and other squid as they grow (Vovk, 1972; Macy, 1982b; Vovk, 1985; Anderson and Griswold, 1988). Alternatively, this difference could be the result of a shift from somatic to gonadal growth as squid mature (Macy, 1995), although this seems less likely given the substantial variability in size at maturity of *L. pealei* (Macy, 1980). Regardless of the cause, understanding the implications of the rapid growth of adults and its relationship to maturity stage will be important for predicting how the population structure will respond to exploitation. Over the longterm, it is conceivable that intensive exploitation of an annual semelparous species, such as *L. pealei*, could lead to strong selective pressure for a smaller average size at maturity. Such a reduction in average size at maturity could diminish the reproductive potential of the population (cf. Murphy et al., 1994), and this could lower resilience to environmental fluctuations by reducing the genetic variation in the population.

The implications of these estimates of growth for *L. pealei* in the northwest Atlantic are substantial for the assessment and management of this resource. The short lifespan for this species, combined with the rapid growth of adults and the capacity to spawn year-round, implies that the stock will respond rapidly to environmental variation and fishing pressure. As a result, monitoring the stock for in-season management would likely require several assessments throughout the year.

New management measures are being developed for the long-finned squid stock to reflect the improved understanding of its growth and pattern of reproduction (MAFMC[6]). At present, management of the stock is based on a level of total allowable catch that cannot be exceeded (MAFMC[7]) and on an overfishing definition that has been characterized as "risky" (Rosenberg et al. 1994). A preliminary analysis of some of the weight-at-age data presented in this study indicated that the annual level of maximum sustainable yield, based upon average recruitment and an initial estimate of maximum yield per recruit, could be roughly 36,000 t (NEFSC[8]). This interim estimate was 18% lower than the estimate of 44,000 t, which was based on a presumed two-year lifespan (Sissenwine and Tibbetts, 1977) that has been used as the maximum optimum yield for the stock (MAFMC[7]). However, this estimate appears overly optimistic because landings above 36,000 t have occurred only once, in 1973, when 37,600 t were landed. Regardless, any revision of the annual level of sustainable yield for the stock will need to account for the seasonal patterns of growth and spawning, the potential discarding of juveniles, and variability in stock-recruitment dynamics. Further, it would be more appropriate to estimate sustainable yield and to develop an overfishing definition on a seasonal, rather than an annual, basis for this short-lived species. In contrast to the current quota-based harvesting strategy, a constant harvest-rate strategy that includes a proportional escapement target (Beddington et al., 1990) on a seasonal basis may be a useful management approach.

If the long-finned squid stock is managed on a seasonal basis, revised stock assessment procedures are likely to require rapid collection of catch and effort data and efficient data analysis during periods of peak fishing activity. Real-time assessment procedures have been used to monitor the short-finned squid stock in Falkland Islands waters during the fishing season to achieve proportional escapement goals (Rosenberg et al., 1990), and the use of a constant harvest-rate strategy is a potential option for management of the long-finned squid resource. Although a constant harvest-rate strategy can be overly restrictive in years of good recruitment and result in a loss of yield, it can also jeopardize the stock when recruitment is poor. Therefore, assessment procedures that permit in-season adjustment of the harvest rate would likely be necessary to maintain an adequate level of spawning biomass if management is conducted on a seasonal basis.

As with any renewable resource, long-term management of the long-finned squid stock will involve a balance of the risks and benefits of harvesting the resource. Because long-finned squid are semelparous and likely live for less than 1 year, the risk of re-

[6] Mid-Atlantic Fishery Management Council. 1995. Amendment 5 to the fishery management plan and the final environmental impact statement for the Atlantic mackerel, squid, and butterfish fisheries. MAFMC, Dover, DE.

[7] Mid-Atlantic Fishery Management Council. 1992. 1993–1994 allowable biological catch, optimum yield, domestic annual harvest, domestic annual processing, joint venture processing, and total allowable level of foreign fishing recommendations for Atlantic mackerel, *Loligo*, *Illex*, and butterfish. MAFMC, Dover, DE.

[8] Northeast Fisheries Science Center. 1994. Report of the 17th Northeast Regional Stock Assessment Workshop. NEFSC Ref. Doc. 94–06, Woods Hole, Massachusetts, 124 p.

cruitment overfishing is substantial for this stock. Further, because growth appears to be nearly exponential throughout its life cycle, the risk of growth overfishing is also considerable. On the other hand, harvesting impacts may be difficult to evaluate unless stock response to environmental variation, density-dependence in growth and survival, and community-level interactions with competitors and predators are better understood. Owing to its short lifespan, the immediate benefits of harvesting the long-finned squid resource are probably best measured by average seasonal yield and its variance, and an adaptive approach to management may be needed to ensure sufficient spawning escapement and to foster efficient utilization of this resource.

Acknowledgments

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